

V.—On the Systematic Position of the Pulicidæ.

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[Plate III.]

AFTER my investigations on the buccal organs of the Diptera and Rhynchota † had led me to the conclusion that in the former the true sucking-tube (not to be confounded with the labium, which serves only as its sheath) was formed by a dorsal and a ventral half-gutter (labrum and hypopharynx), and in the latter by two double half-gutters laterally interlocked, it seemed natural to study also the aberrant members of the two series in the light of this criterion, which applied to all typical forms, in order to arrive at greater clearness with regard to their relationships. In this respect no small interest undoubtedly attaches to the group Pulicidæ, which, notwithstanding much difference of form, presents such a uniformity of organization, and as to the systematic position of which for more than a century the most different opinions have been expressed, without any generally acceptable and well-established view having yet been arrived at.

The history of these opinions has already been given pretty completely by Taschenberg in his Monograph on the Fleas ‡, so that here a short recapitulation may suffice.

Linné, as is well known, created an order Aptera for the wingless insects, Myriopods, Spiders, &c., and in this the flea found its place. A similar position was assigned to it by Geoffroy, Cuvier, and Duméril, as also by Gervais; while, on the other hand, the order Aptera was by many rejected as unnatural, and the relationship of the Pulicidæ with various winged insects was asserted. Thus Kircher referred them to the Orthoptera, Fabricius and Illiger to the Rhynchota, Rösel, Oken, Strauss-Durckheim, Newman, Burmeister, Walker, Von Siebold, and others to the Diptera. Lastly, there were also very early naturalists who would associate the flea with none of the existing orders of insects, but postulated a distinct order for it. The leader in this direction is De Geer. He was followed by Lamarck, Latreille, Kirby and Spence, MacLeay, Leach, Dugès, Bouché, and Van der Hoeven, and,

* 'Festschrift zum 50-jährigen Jubiläum des Realgymnasiums des Johanneums,' Hamburg, 1884. Translated by W. S. Dallas, F.L.S.

† In part set forth in the preliminary communication "Ueber die Mundwerkzeuge der saugenden Insekten" (Zool. Anz. 1882, pp. 574-79) and in a memoir, "Zur Anatomie und Physiologie des Rüssels von Musca" (Zeitschr. f. wiss. Zool. xxxix. pp. 683-719).

‡ Taschenberg, 'Die Flöhe' (Halle, 1880).

among later investigators, by Landois and Taschenberg. But although the last two authors especially pronounced most decidedly in favour of the independent position of the Fleas in the system, and although the most accepted special works upon the Diptera exclude the Fleas as not belonging to the series of forms in that order *, we find that even in the most recent manuals of zoology the group of insects in question is almost without exception cited as a suborder of the Diptera. This may pass in the first place as a proof that really stringent arguments have not yet been brought forward in favour of either view ; but we might also derive the hesitation felt by many zoologists to raise the rank of the Fleas (even under otherwise sufficient grounds) from the circumstance that they lead a *parasitic* existence, and by this means have possibly undergone profound and peculiar morphological changes by "adaptation," as is sufficiently established for other groups of parasitic forms. In opposition to this, however, it must be remembered that with only isolated exceptions (the females of the Sarcopsyllidæ) the Pulicidæ are not stationary, but only *temporary* parasites, that their whole development is completed without parasitism, and that therefore we cannot well assume any considerable adaptation to a parasitic mode of life. But if this be so, if we succeed in proving that the Pulicidæ possess a series of morphological characters which cannot be regarded as acquired by parasitism, we must necessarily, in judging of their position in the system, consider the same points of view to be prescriptive that have been generally adopted for the establishment of orders, suborders, and families in the class of insects.

These general points of view, however, do not offer us a very brilliant prospect. The Linnean *principium divisionis*, the form, number, and texture of the wings, having proved to be untenable, we find on the one hand the kind of transformation and its various stages, and on the other the structure of the organs of the mouth, raised into the most important criteria of the nearer or more distant relationship of the groups of insects. But, as is always the case, when a single character is thrown too much into the foreground, and the general morphological relations of the two series of forms are not allowed to be prescriptive, difficulties make their appearance even with these apparently so thorough-going principles of division, which considerably diminish their value. The

* It is interesting that the well-known work on the Diptera of the 'Fauna Austriaca' by Schiner certainly expresses itself decidedly enough in the above sense, but then gives a definition of the true Diptera, which might very well embrace the Pulicidæ.

group of the Orthoptera, which is certainly not very natural, and their multifarious relations with the Neuroptera, the suctorial Apidæ, the biting Mallophaga, and lastly the pupal rest of the male Coccidæ, may sufficiently establish this proposition. It is still worse, however, as regards general availability, with the distinctive characters of the orders generally cited—the segmentation of the thorax and tarsi, the structure of the wings, of the different buccal organs, antennæ, &c. The mere fact of the agreement or difference of these organs individually cannot give us certainty as to the systematic relationship of two series of forms, but only the examination whether the general organization of one group, as expressed in the development of all morphological characters, shows or does not show *phylogenetic relations* with those of another group; in other words, whether the observed differences in the structure of the parts may be referred equally well to a different “fundamental plan” in their arrangement, as to simple changes of form and reductions, such as may be explained by altered function. Self-evident as this proposition appears in the light of modern zoology, the history of opinion as to the systematic position of the flea nevertheless shows very plainly how little it has hitherto been taken into consideration by entomologists. One important aid in such investigations upon the true phylogenetic relationships of forms is unfortunately at present still almost wholly shut out from us. I refer to the anatomical structure of the organs. The knowledge of this, and especially that of the generative organs, is at present so imperfect that a detailed consideration of the internal organization seems to be of little use in the classification of insects.

After these prefatory remarks upon the principles which are or should be of force in the grouping of insect-forms, the question as to the systematic position of the Pulicidæ may be postulated as follows:—Do they or do they not, in the totality of their organs, show near relations of affinity with any of the other groups of insects? In the former case we should have to arrange them in this group of insects; in the latter we must establish an independent order for them.

I naturally commence my examination with that order of insects which, in the judgment of zoologists, has the most right to receive the Pulicidæ into it, namely the Diptera. The series of the Diptera must decidedly be called a unitary one; but the two characters so often brought prominently forward (a perfect metamorphosis and suctorial buccal organs) do not alone establish this unity, seeing that we must also ascribe them to the Lepidoptera, the Apidæ, and the male

Coccidæ. Nay, even if we add the footless larvæ and the fusion of the thoracic segments as further criteria, we might perfectly well unite the Bees with the Diptera. It is not the simple fact of the suctorial buccal organs that is of importance, but their specific structure, the position and arrangement of the parts composing the suctorial apparatus. If we fix our attention upon this point we at once recognize that the fly's proboscis is constructed upon a perfectly different fundamental plan from that of the Apidæ, that the two are not directly phylogenetically referable to each other, but that, on the other hand, the great variations in the buccal apparatus of the Diptera only represent modifications of one and the same type, distinctly demonstrable throughout. The characteristic of the bee's trunk consists in the development of the *lower* parts of the mouth into the sucking organ, while the mandibles retain their original function; that of the fly's proboscis, on the contrary, in the employment of the labrum and hypopharynx for the formation of the sucking-tube, with which the mandibles and maxillæ associate themselves as stylets more or less developed as required, while at the same time the labium in all cases has to form a protective sheath for the comparatively delicate tube through which the fluids ascend. This fundamental plan of the employment of the parts of the mouth occurs, as already pointed out in the introduction, in all the groups (except the Pulicidæ) which have hitherto been placed in the group Diptera, in the piercing Culicidæ, Tabanidæ, and Asilidæ, the different families of honey-suckers, and the Pupipara, which are so depressed in position through parasitism; nay, a bridge seems even to be thrown over towards the rudimentary buccal organs of the Cæstridæ, through the structures which occur in *Cuterebra*. In figs. 1-3 (Pl. III.) I have drawn transverse sections of the proboscides of those groups of flies which, upon one hand or the other, have been referred to as allied to the flea. While those of *Tabanus* and *Culex* (figs. 1 and 3) agree not only in the position but also in the number of the pieces composing the proboscis, that of *Melophagus* (fig. 2, the representative of the Pupipara) shows a great reduction, which finds its expression in the entire absence of the mandibles and maxillæ*; but

* The two valves embracing the proboscis of the Pupipara have been very erroneously interpreted as maxillæ, their palpi, or even as a bipartite epipharynx (Meinert). From the whole arrangement of the proboscis, which is freely movable in a wide cavity of the head extending as far as the prothoracic ring, we can here have to do only with a conical prolongation of the head which has become paired, somewhat such as we should obtain if we imagined the slight emargination at the apex of the frontal cone of *Rhingia* carried down to its base. The strongly projecting cheeks of many Conopidæ might also perhaps be regarded as analogous.

nevertheless it is easy even here to recognize the typical position of the pieces forming the sucking-tube (dorsally the labrum and ventrally the hypopharynx), and the labium which encloses these as a sheath. Further, the latter bears at the end that enlarged portion which is so characteristic of all Diptera, and which is probably to be interpreted as formed by uniaarticulate labial palpi.

The same unity in the Diptera appears also in the special structure of the thorax and its appendages. That this appears always separated from the head by a deep incision is certainly not without significance; but it can furnish no decisive datum for the collocation of the Diptera. Of more importance, no doubt, is the fusion of the thoracic segments into a compact thoracic mass, which occurs in all the forms referred to this group. It is indeed true that in orders of insects (I refer particularly to the Rhynchota) the formation of the thorax as regards the separation or fusion of the segments composing it shows manifold differences, without its being necessary that we should separate forms which are united for other reasons, seeing that the fusion or separation of the thoracic segments has to do essentially with a function of the mechanism of flight, and the free segmentation of the thorax in a wingless form may very well be explained as a correlative phenomenon of adaptation. But the conditions are different if, on the contrary, a wingless form exhibits complete amalgamation of the thoracic segments. In my judgment it thereby demonstrates most unmistakably its descent from winged insects, and in this sense the compact structure of the thorax, with the characteristic process of the mesothorax described as the "scutellum," in *Melophagus*, the Nycteribiidæ, and the Braulidæ, decidedly acquires the significance of a still uneffaced relationship with the winged groups standing next to them. And just as on account of this character the assumption is justified that the forms just mentioned stand in close phylogenetic relationship with winged insects, so does the examination of the dorsal appendages of the thorax lead to the same conclusion. All Diptera do not possess a pair of wings and a pair of halteres; but the two organs which, because special, are certainly of such great importance in characterizing the Diptera, disappear so gradually in the continuous series of forms, that we may trace their progress to the rudimentary state, as it were, step by step. An *Ornithobia pallida* which, as *Lipoptena cervi*, follows a perfectly different mode of life, enables us at once to understand the case, when we see *Melophagus*, which is never parasitic upon birds, entirely destitute of wings. But as regards the

halteres, these, notwithstanding Schiner's assertion to the contrary, are quite recognizable in the sheep-tick, while in the Nycteribiidæ they show all gradations down to quite minute points, so that the complete absence of these apparently insignificant organs in the Braulidæ need not give us any further disturbance. The *ventral* thoracic appendages, the legs, certainly present but few differences in the group of the Diptera, nevertheless the five tarsal joints which are usually present are not always constant; and further, other orders of insects sufficiently prove how little importance attaches in general to the number of tarsal joints and the development of the different sections of the legs.

The *developmental stages* of the Diptera do not show a community of type so distinctly as the structural characters just referred to. The larvæ are certainly throughout distinguished by the absence of jointed thoracic limbs, which is of special interest in the case of those forms which live free upon leaves by prey (many larvæ of Syrphidæ); but with regard to the structure of the head, the armature of jaws, and the development of the tracheal system, there are, as is well known, such important differences, that they have been successfully employed for the systematic division of the order into several suborders and sections. Nevertheless even here intermediate grades are not wanting between the different structural characters (witness the variable development of the first cephalic segment); nay, in Brauer's* opinion, the family Lonchopteridæ may possibly prove to be a perfect transitional group between the Orthorapha and Cyclorapha, so that the multifarious forms of the larvæ at least offer no veto against the unitariness of the stem of the Diptera. The same thing can also be said of the pupæ, which indeed likewise fall under two main types, but are so far brought together by Brauer's investigations, that these furnish a proof that the so-called "tun-pupæ" (obtect pupæ) show very different grades of structure, and in many of them the enveloping larva-skin bursts exactly as in the ordinary moulting, and consequently is to be referred simply to a delayed moulting at the close of the larval period. In the latter case, moreover, if the appendages of the segments of the body are not so closely attached to each other and to the body as in the naked and consequently less protected and more easily injured "mummy-pupæ," no important objection against the natural relationship of the two groups can be derived from this circumstance, which evidently results from

* F. Brauer, 'Die Zweiflügler des Kais. Museums in Wien,' p. 9 (Vienna, 1883); also in the Denkschr. d. math.-naturwiss. Klasse d. k.-k. Akad. d. Wiss. Bd. xlvii.

altered condition. The "mummy-pupæ," however, show many differences among themselves with regard to the closer or looser appression of the appendages of the body, as may be demonstrated by a comparison of the pupæ of the Asilidæ, which rest in the ground, and those of *Tipulæ* which live in the water.

Of anatomical peculiarities of the Diptera especial mention must be made of the "sucking-stomach," which is always present, as also of the large thoracic salivary glands, the efferent ducts of which, wherever the buccal organs perform any function, unite into an unpaired closed canal, which, running along in the cavity of the hypopharynx, opens at its extremity. The testes are almost always two; the Malpighian vessels almost as regularly four. As regards the tracheal system, the constant absence of the first thoracic stigma and the small number of abdominal stigmata are to be noticed; while the nervous system, as is well known, shows all possible forms of development, from the most extreme concentration to a very considerable segmentation of the ganglionic chain.

If we turn from this brief account of the Dipterous type to the characters of the Pulicidæ, we must admit, in the first place, that in a whole series of points of comparison an agreement between the Diptera and the Fleas can be demonstrated. Like the Diptera, the Fleas have a suctorial buccal apparatus, a perfect metamorphosis, and footless larvæ; as in them also the tarsi are five-jointed, there are four Malpighian vessels, and one pair of testes. But, as has already been indicated at page 38, we could only ascribe decisive weight to this agreement if all these characters were peculiar to the Dipterous stem alone, and if at the same time, by more detailed comparison, real tenable parallels could be drawn between the different parts of the organs, as between the different stages of development. This, however, is by no means the case. The number of Malpighian vessels and of testes recurs in the same way in the Rhynchota, and therefore proves no more in favour of the relationship between the Fleas and the Diptera than the number of the tarsal joints or the annulation of the terminal knob of the antennæ, which may be recognized in all possible groups of insects. At the first glance more importance seems to attach to the agreement of the two groups in the larval state, which in fact goes so far, that Brauer* has no hesitation about arranging the larva of the flea in his group of orthoraphal eucephalous Dipterous larvæ. In opposition to

* Brauer, "Kurze Charakteristik der Dipterenlarven," in Verh. k.-k. zool.-bot. Ges. in Wien, 1869, p. 846.

this, however, we must not forget that maggot-like larvæ also occur in groups far removed from the Fly-type, in Hymenoptera and Beetles, and therefore cannot possibly be of decisive importance in judging of relations of affinity; as also, on the other hand, that the pupa of the Fleas with its quite separate limbs differs so much at least from the general type of the mummy-pupæ, that from this very fact it has been attempted to set up a relationship of the Fleas to the Hymenoptera*. Hence the point of the question how far the analogous characters in Diptera and Pulicidæ depend upon true phylogenetic affinity would have to be sought in the investigation whether the construction of the sucking-apparatus is carried out in both cases on the same plan, *i. e.* with the same employment of homologous parts. That it is only from this discussion and from that as to the structure of the thorax and its appendages that a real decision of the question before us can be arrived at, may indeed be deduced from the consideration that in these organs we find the only characters which, on the one hand, are confined to the order Diptera, and, on the other, may be traced throughout their whole series of forms, and therefore must be regarded *κατ' ἐξοχήν* as typical.

The structure of the buccal apparatus of the Pulicidæ has been very frequently discussed without the question of its relationship to the sucking-apparatus of other groups of insects having as yet been solved. Thus to cite only a few:—Dugès† thinks that the proboscis of the flea may be placed side by side with that of the Tabanidæ, but also finds resemblances to the Hippoboscidæ and Apidæ. L. Landois‡ suggests a resemblance of the mouth-apparatus of the Pulicidæ to the rostrum of the Hemiptera; while Taschenberg§, again, thinks he recognizes the Dipterous type, and especially calls attention to the presence of a “tongue” as the most characteristic part of the mouth of a fly. This extraordinary diversity of opinions is principally to be ascribed to the uncertainty of the interpretation of this very “tongue” of Taschenberg’s. The mandibles, maxillæ, and labium have long since been recognized with certainty; but the unpaired piercer” (to express myself neutrally) has been referred to as the labrum (Westwood, Haller, Bonnet), as the hypo-

* As by Dugès, in his “Recherches sur les caractères zoologiques du genre *Pulex*,” in Ann. Sci. Nat. tome xxvii. p. 157.

† *Loc. cit.* p. 151.

‡ L. Landois, “Anatomie des Hundeflohes,” in Nova Acta Acad. Leop.-Car. 1866, p. 56.

§ *Loc. cit.* p. 41.

pharynx (Gerstfeldt), as the epipharynx (Karsten), and lastly, as already mentioned, as the "tongue" (Savigny, Taschenberg), and therefore all serious homologizing must have been prevented, the more, as even the real components of the sucking-tube were not made out with certainty.

In figs. 10 and 13 I give two transverse sections through the anterior part of the Pulicid proboscis. Fig. 10 represents a section from *Pulex irritans*; fig. 13 a similar section, but nearer the base of the proboscis, from *Sarcopsylla penetrans**. The sections show at once that the structure of the sucking-tube in the two most distant groups of the Pulicidæ is quite accordant. In both cases it is the mandibles (*md*), which, in conjunction with the "unpaired piercer," form the true food-canal; embracing the latter above and laterally, they join firmly together in the median line below. A glance of comparison at figs. 1-3 shows that this "unpaired piercer" is hollowed into a groove on the underside exactly in the same way as the *labrum* of the Diptera, and that to begin with there is no hypopharynx, but at the utmost perhaps an epipharynx. But if we trace the further course of this structure by the aid of longitudinal and transverse sections it is easily seen that its upper covering immediately after its entrance into the capsule of the head is in chitinous union with the upper margin of the arch of the head, while the inferior plate, *i. e.* the one which immediately forms half the sucking-channel, passes continuously into the chitinous covering-wall of the pharynx. Consequently we find in the organ in question precisely the same conditions as in the labrum of the Diptera, and there is no doubt at all that we have to do here with a true labrum. A connexion of this with the labium by means of a strongly chitinized, brown uniting piece, as asserted by Dugès (*l. c.* p. 150), really has no existence at all†, and this removes the last possibility of regarding this structure as a "tongue," *i. e.* as an extension or appendage of the labium.

The interpretation of the "unpaired piercer," as labrum, being thus established beyond a doubt, the comparison of the proboscis of the flea with that of the Diptera can present no further difficulties. The employment of the labrum (*l*) as the unpaired covering lamella of the food-canal is apparently the same in both groups. But it is otherwise with the other components of the sucking-tube. In place of the horizontally-

* The material was kindly sent to me from Assumption by my honoured colleague Dr. H. Töppen.

† This chitinous piece rather forms the lever for moving the mandible, as will be shown elsewhere.

placed mandibles of the Tabanidæ and Culicidæ, which, as is proved by those Diptera which do not pierce, are only secondarily implicated in the closure of the sucking-canal, we see in the Pulicidæ the vertically-placed mandibles, bent in towards each other laterally, appear as integral parts of that tube—a different inferior closure, such as exists in the hypopharynx throughout the whole group of the Diptera, being here entirely deficient. This absence of the hypopharynx, which, as is clear from what has been said, has as its consequence a totally different importance of the mandibles, and consequently a perfectly peculiar type of sucking-tube*, proves in like manner of importance as regards the discharge of the salivary glands. The unpaired salivary duct in the lumen of the hypopharynx is replaced in the Pulicidæ by paired extremely fine half-tubes (fig. 13, *s*), each of which, running along the inner side of a mandible, may be traced from the basal part of the latter as a closed duct into the interior of the head, and, further, as far as the thoracic salivary gland †.

Equally great differences in their arrangement and physiological importance may be demonstrated by a comparison of the other constituents of the proboscis of the flea with the homologous organs of the Diptera. A labium unpaired throughout its whole length, and at the utmost furnished at its apex with one-jointed terminal lobes, occurs nowhere among the Pulicidæ, although something of the kind was formerly ascribed to *Sarcopsylla*. The labium of *Sarcopsylla* at least presents (as fig. 8 may show) a biarticulation of the “palpi,” even with an indication of further segmentation, so that in this point also the unity of the Pulicide group appears. This difference of the segmentation of the labium in Diptera and Fleas, with which a typical difference in the relative length of the unpaired basal part to the paired section to be regarded as palpi, goes hand in hand, can, however, hardly be so highly estimated in its phylogenetic significance as the further fact that the labium of the Diptera shows quite a different attachment to the head, and so has quite a different physiological value from that of the Pulicidæ. In the former it generally attaches itself by its gradually widening base to a more or

* Particular attention may here be directed to the two peculiar lateral lamellæ of the labium, which apparently, by their elasticity, force the upper parts of the mandibles asunder, and thus bring about a closer apposition of their lower parts.

† Kraft and Landois believe that they have demonstrated an opening of the thoracic salivary glands into the œsophagus not far from the region of the neck (see Landois, *l. c.* p. 18).

less developed cephalic cone, with the upper lateral parts of which it is connected, and so is enabled from the base onwards to form that sheath of the delicate piercing apparatus (the two pairs of jaws as well as the labrum) which often arches together above so as to constitute almost a closed canal. In the Fleas, on the contrary, there is no such union of the labium with the lateral or upper parts of the head; it simply articulates with a firm brown chitinous piece (fig. 9, *ch*) in the median line of the lower surface of the head, and this union, as is well known, is frequently so loose that it is difficult to obtain *Sarcopsylla*, for example, with the labium preserved*. Hence, in its basal part, it does not form the sheath for the piercing-apparatus, but shows only a comparatively shallow groove (fig. 15), which only in the anterior section of the proboscis, when the stem of the labium has become cleft into the paired palpi, becomes developed, at least in *Pulex*, into two flaps, embracing the piercing-organ at the sides (fig. 10, *lp*). But to make up for the deficient protection of the basal part of the sucking-tube (and in this we have a fundamental deviation from the type of the Diptera) the maxillæ have come in, originating as two broad plates from the whole length of the side of the head, and taking here, not only the constituents of the piercing-apparatus, but also the base of the labium, under their protection, as shown by fig. 15 in *Pulex*.

We seek in vain for analogies to all these characters among the Diptera, and we may therefore be justified in asserting that all the parts of the Pulicide proboscis (with the sole exception perhaps of the labrum) differ so much in position and employment from the homologous parts in the Diptera, that we cannot well speak of direct phylogenetic relations between the two types of proboscis.

We arrive at precisely similar conclusions as to the relationship of the Pulicidæ and Diptera when we take into consideration the second group of characters peculiar to the Diptera, which appear in *the structure of the thorax and its dorsal appendages*. Instead of the always freely movable head of the Diptera, we find a broad union of it with the prothorax in the Pulicidæ; instead of the compact thorax with its scutellum, which is so characteristic even of the wingless Pupipara, we have three sharply separated thoracic segments, without a trace of any such dorsal mesothoracic process; and instead of the pair of wings and the halteres, the latter of which are aborted only in the most extreme cases of parasitism,

* Even in recent handbooks we may find the statement that the labium of *Sarcopsylla* is indistinct.

there is *nothing*, absolutely nothing, that could lead us to conclude that the Fleas were formerly in possession of any such organs. Even the marked tripartite condition of the thorax ought *à priori* to have banished the idea of rudimentary wings; nevertheless the older authors (Kirby, Dugès, &c.) have fallen into the serious error of regarding separated lateral margins of the thoracic segments as such. But these "processes of the pleuræ," as Taschenberg * among others has conclusively proved, have nothing at all to do with wing-rudiments, and are to be regarded as characteristic structures *sui generis*. When Taschenberg therefore for this reason declares the generally-employed denomination of "Aphaniptera," founded upon this erroneous conception, to be inadmissible, we can only agree with him. It is only by giving up this name that we can seriously hope that the deeply rooted notion of the "Diptères sans ailes," as Strauss-Durckheim called the Fleas, will be completely suppressed.

The wide gap which exists precisely in the most important characters between the Pulicidæ and the Diptera must have been made sufficiently evident by the preceding remarks. That it is also expressed in other systems of organs than those hitherto considered may therefore only be briefly indicated. The sucking-stomach, which apparently is met with in all groups of Diptera, is entirely wanting in the Pulicidæ; while, on the other hand, the proventriculus beset with numerous chitinous spines of the latter has no analogy among the Diptera. The sucking-mechanism of the pharynx or of the so-called "fulcrum" of the Diptera is formed by a single powerful pair of muscles; in the Fleas, on the contrary (as in the Rhynchota), a whole series of separate pairs of muscles (which, however, are interpreted by Landois as flexors and retractors of the labrum) are present for this function. Lastly, the presence of a stigma in the prothorax of the Fleas indicates more profound differences in the tracheal system; while as regards the simple ocelli of the Pulicidæ and the deep lateral pits of the head, we may find analogous phenomena among the Rhynchota, but not among the Diptera.

After all this the Fleas cannot well remain in the order Diptera. There remains then the investigation of the question whether they show near relations to any of the other groups of insects. Hymenoptera and Orthoptera, of which earlier authors have thought in this connexion, cannot well come into the question in the present state of our knowledge, as it would be opposed to all rational system to assert a rela-

* *Loc. cit.* p. 21.

tionship of the Fleas to the Hymenoptera upon the sole accordance of the pupæ, or to the Orthoptera upon the segmentation of the thorax. The order Lepidoptera also cannot agree in a single one of the more important characters with the Pulicidæ, and thus there remains only the group Rhynchota for serious comparison. As a matter of course, considering the fundamental difference of development between Pulicidæ and Rhynchota, we can hardly expect to find real intimate relations between the two groups, at least not so close as we must postulate for forms of one and the same order; nevertheless I think I may indicate some points of view which deserve to be well considered in judging of the phylogenetic connexion between Fleas and Rhynchota.

In the first place there can be no doubt that the order Rhynchota does not even approximately present a unitary type in the same degree as that of the Diptera. We find united in it animals with suctorial and masticating buccal apparatus, with perfect, imperfect, and without metamorphosis. The head is sometimes freely movable, sometimes attached by a broad surface to the prothorax. The thorax, so very uniformly constructed in the Diptera, shows all possible stages of structure, from the enormous development of the separated prothorax in Scutata and Membracina, to the compact thorax showing scarcely an indication of segmentation of the Pediculina, or that of many Mallophaga more or less sharply divided into three distinct segments; and like the thorax itself, its dorsal appendages also present no unity of type. With such polymorphism of almost all organs it is easily intelligible that we should be able to find in this Protean group analogies for a whole series of characters of the Pulicidæ. Thus the segmentation and winglessness of the thorax in the Fleas may be without difficulty placed side by side with the similar conditions among the Mallophaga, which, at the same time, present examples of the antennary pits of the head already mentioned. The absence of faceted eyes in Pulicidæ agrees with what occurs in Coccidæ, Pediculina, and Mallophaga, the pupa enclosed in a cocoon unites them with the Coccidæ; the absence of sucking-stomach and the number of the Malpighian vessels and testes are even common to them and to all forms of Rhynchota.

For the reasons above given, however, we must not ascribe a serious significance to all these agreements unless the Rhynchotan type sought for finds expression at least in the last of the characters to be discussed, those of the buccal apparatus, and shows near relations to the homologous organs of the Fleas. According to the present state of our know-

ledge it cannot well be maintained that there is a clear unitariness of structure in the buccal organs of the Rhynchota, as, at any rate among the Apteræ (the Pediculina and Mallophaga), conditions occur which depart widely from those of the more highly organized groups. But as the arguments upon this point are not yet closed and I have made no investigations upon these lower forms, we must content ourselves with examining at least the sucking-apparatus of the Hemiptera and Cicadæ in search of any agreement with the proboscis of the Fleas that may exist. With regard to the arrangement of the parts of the mouth in these higher groups of the Rhynchota, I have already published some statements in a previous note *, and these observations have since been confirmed and extended by Geise †. According to these the true sucking-tube of the proboscis is formed by the two maxillæ closing laterally against each other into a double tube, while the mandibles are placed alongside of this tube as lateral piercing-setæ. From more recent investigations I do not hesitate to declare this view ‡ so far erroneous that it is not the *maxillæ* but rather the *mandibles* that interlock in the median line to form the sucking-tube (see figs. 11, 14). I am led to this changed interpretation of the two pairs of jaws in the first place by the fact that in transverse sections through the head the *lateral* setæ finally come to be the lower ones, as, indeed, Geise correctly shows in his figs. 25 and 31. Secondly, I think that in the Cicadæ I have found distinct traces of basal joints of the maxillæ connected with the *outer* setæ. Fig. 12 shows the lower part of the face of a large tropical Cicada. On each side of the broad labrum (*br*) there is here an oblong plate (*pl*), which terminates almost in the middle line beneath the labrum in a blunt hairy tubercle and a peculiar whip-like appendage (fig. 6, *f*). If this structure be prepared out of the head, a connexion, certainly only by articulation, with the lateral piercing setæ may be easily demonstrated, for protrusion and retraction of which not only the chitinous sinews (fig. 6, *sp* and *sr*), but also the corresponding muscles (fig. 6, *pm* and *rm*) are attached to this chitinous piece. If this interpretation of the chitinous piece occurring in all Cicadæ, Fulgorinæ, &c., as the basal part of a jaw, perhaps even with palpiform appendages, be correct, this must, of

* Zool. Anzeiger, 1882, p. 574.

† Geise, 'Die Mundtheile der Rhynchoten' (Bonn, 1883).

‡ On my part this resulted merely from what I now believe to be a wholly unjustified homologizing with the buccal organs of the Lepidoptera, the sucking-tube of which is undoubtedly formed of the maxillæ (see also Kirbach, Zool. Anz. 1883, p. 553).

course, be a maxilla, and thus the composition of the sucking tube out of the two mandibles would be finally decided. But then we should at once be enabled, in *one* point, to carry on a corresponding comparison between the buccal organs of the Pulicidæ and Rhynchota, inasmuch as we need only suppose the labrum of the latter, which is indeed often enough developed into a long, slender, stylet-like organ, to sink from above between the mandibles*, in order to arrive at conditions which might perfectly well be placed side by side with those occurring in Pulicidæ (compare fig. 11 with fig. 15). It appears further that upon the basis of my conception a connexion might be established between the modes of discharge of the saliva in the Pulicidæ and Rhynchota, if we assume that the paired half-grooves along the inner side of the mandibles of the Pulicidæ (fig. 13, *s*) have coalesced in consequence of the changed adhesion of these jaws, caused by the emergence of the labrum, as a constituent of the sucking-tube, into an unpaired efferent canal (figs. 11 and 14, *s*). The variable part taken by the two mandibles in Hemiptera and Cicadæ (see fig. 14) in the formation of this salivary tube would come in support of this hypothesis. Among the Rhynchota, as is well known, a hypopharynx is not developed as a separate organ, or only as a rudiment (in Cicadæ), so that in this circumstance also a parallelism between Pulicidæ and Bugs may be found.

The *labium* of the Rhynchota consists of four consecutive cylindrical joints furnished with a deep longitudinal groove along the upper surface. It has been said that it is destitute of palpi, but I think that this mode of expression is not correct. A labium divided into four or five successive rings is in complete contradiction to the plan of the organ deduced from the consideration of the masticating mouth. But notwithstanding Geise's assertion to the contrary (*l. c.* p. 11), there is nothing to prevent our regarding the cylindrical and often much more voluminous basal part of the labium as the submentum and mentum, as a direct continuation of which arise the multiarticulate palpi fused together in the median line. That there is really an amalgamation in the terminal joint of the labium is rendered probable by the circumstance that both in the Hemiptera and in Cicadæ a pretty

* Geise asserts something of the kind when he represents the labrum in *Corixa* and *Sigara* as taking part with the constituents of the sucking-tube (*l. c.* p. 53, fig. 29); unfortunately I must reject this assertion—welcome as it would be to me for the homology attempted above—as positively erroneous.

considerable notch appears at the apex*, although the side lobes thus produced are not jointed off from the unpaired piece in the same way as is usually the case, with the labella of the Diptera for example. But if this conception of the structure of the labium of the Rhynchota be correct, a comparison of it with that of the Pulicidæ presents no difficulties. A fusion of the longitudinal fissure of the labium of *Sarcopsylla* (fig. 8), for example, nearly to the apex, would essentially realize for us the conditions existing in Rhynchota (compare the labium of Cicada in fig. 5). And with this apparent equivalence of the parts an approximately similar physiological application of them would be associated.

It has already been pointed out that the labium of the Pulicidæ has undertaken the guidance of the sucking-tube only in its distal and not in its proximal part. But exactly the same thing may be asserted of the labium of the Rhynchota, which in the basal section of the rostrum shows an effacement of the dorsal furrow and decidedly turns downwards, and thus devolves the guidance of the sucking-canal and of the piercing setæ entirely upon the labrum. In the latter circumstance, indeed, there is an essential difference between the proboscis of the Fleas and that of the Rhynchota, as in the former the labrum, which has become one of the constituents of the sucking-tube, cannot possibly be employed to envelop the whole apparatus. But precisely this different application of the labrum renders intelligible a further fundamental difference between the two types of proboscis, which must be found in the physiological application of the maxillæ. In the sucking-tube of the Rhynchota, which, under the double guidance of the labium and labrum, is sufficiently enveloped and protected throughout its whole length, the maxillæ might, without damage, be brought in to complete the true piercing-apparatus; they have become long thin structures, destitute of palpi, flanking the sucking-tube. In the Pulicidæ, on the contrary, in which the basal section of the sucking-tube, in consequence of the peculiar employment of the labrum, was destitute of an envelope, the maxillæ, developed into broad plates (figs. 4 and 7 and 15, *m*), had this important function of protection transferred to them. That under such a change of function the palpi

* The section across the tip of the rostrum of *Notonecta* (fig. 14) shows the labium as consisting of two perfectly separate parts. Geise's statement that in *Corixa* the third and fourth joints of the labium are completely cleft, depends, according to my investigations, upon an erroneous interpretation of the conditions coming into view at the tip of the rostrum.

also came to full development and importance, can hardly be regarded as a serious obstacle to the homology here attempted.

The preceding indications will suffice to prove that in fact, without any great violence to the data given, a certain parallel may be drawn between the buccal organs of the Fleas and those of the higher Rhynchota, and that this comparison is at least far easier to carry out than that between the Pulicidæ and the Diptera. If we bring the other agreements and differences of the three groups in question into the account, the result must be a phylogenetic alliance, although a distant one, of the Fleas with the Rhynchota rather than with the Diptera. But I repeat that the demonstrated relations certainly by no means justify a union of the two groups. The only possibility that presents itself is therefore to place the Pulicidæ as an equivalent order Siphonaptera* side by side with the two most nearly allied orders.

The entire series of insects with suctorial mouth-organs would consequently have to be divided in the first place into two groups, one of which (Hymenoptera, Lepidoptera) is characterized by having the lower parts of the mouth, maxillæ, and labium employed in the formation of a sucking-apparatus, while in the other, on the contrary, it is almost exclusively the upper parts (labrum and mandibles) that are implicated in the formation of the true food-canal. This latter group would include the three orders Diptera, Siphonaptera, and Rhynchota, which I may, in conclusion, briefly characterize as follows:—

1. DIPTERA. Insects with perfect metamorphosis. Head free, with faceted eyes. Sucking-tube formed by a dorsal and a ventral half-channel (labrum and hypopharynx), more or less enclosed throughout its length by the labium, which is bent up like a sheath and furnished with uniarticulate apical palpi. Mandibles deficient or styletiform, pushing in between the labrum and hypopharynx. Maxillæ, when present, with palpi. Salivary efferent duct an unpaired closed canal in the interior of the hypopharynx. A "sucking-stomach." Thoracic segments amalgamated, usually with a pair of wings and a pair of halteres.

2. SIPHONAPTERA. Insects with perfect metamorphosis. Head attached to the thorax by a wide surface, without faceted eyes. Buccal organs suctorial. Sucking-tube formed

* As the name "Aphaniptera" is inadmissible for reasons already given, and that adopted by Taschenberg, "Suctoria," has already been employed twice, for a group of Cirripedes and for the Acinetæ, I think it best to fall back upon Latreille's name "Siphonaptera."

by a dorsal and two lateral channels (labrum and mandibles), its anterior section only more or less enclosed laterally by the multiarticulate terminal palpi of the labium, and at the base, besides the latter, by the lamelliform palpigerous maxillæ. Salivary efferent ducts paired, developed as a channel along the inner surface of the mandibles. No "sucking-stomach." Thoracic segments free, without wings and halteres, with pleural processes upon the last two segments.

3. RHYNCHOTA. Insects usually with imperfect metamorphosis. Head free or broadly united to the thorax, with or without faceted eyes. Buccal organs usually suctorial. Sucking-tube (in the higher groups) composed of two lateral half-channels (the mandibles), only in the anterior portion enclosed by the labium and its apical multiarticulate palpi, which are united nearly to the apex; at the base by the labrum. Maxillæ styliform, without palpi, applied laterally to the mandibles in the channel of the labium or the labrum. Salivary efferent duct unpaired, formed by two half-channels of the mandibles closing together from the sides. No "sucking-stomach." Thoracic segments free or amalgamated. Four, two, or no wings; no halteres.

EXPLANATION OF PLATE III.

The letters in all the figures refer to the same parts:—*lr*, labrum; *md*, mandibles; *m*, maxillæ; *mt*, maxillary palpi; *l*, labium; *lp*, labial palpi; *h*, hypopharynx; *n*, food-canal; *s*, salivary duct.

Fig. 1. Transverse section through the proboscis of *Tabanus*, sp., anterior third.

Fig. 2. Transverse section through the proboscis of *Melophagus ovinus*, middle.

Fig. 3. Transverse section through the proboscis of *Culex pipiens* ♀, middle.

Fig. 4. Maxilla of *Sarcopsylla penetrans*, side view.

Fig. 5. Labium of *Cicada*, sp., side view.

Fig. 6. Lower part of the maxilla of *Cicada* sp., and its union with a lamelliform appendage (*pl*) of the fore part of the head. *f*, whip-like process of the plate; *pm*, protrusor; *rm*, retractor of the maxilla; *sp* and *sr*, the sinews belonging to them. At *x* the sinew of the protrusor articulates with a chitinous rod which is perpendicular to the surface of the plate, and therefore does not appear distinctly in the figure.

Fig. 7. Maxilla of *Pulex irritans*.

Fig. 8. Labium of *Sarcopsylla penetrans* from above.

Fig. 9. Labium of *Pulex irritans*, side view. *ch*, basal chitinous piece.

Fig. 10. Transverse section through the proboscis of *Pulex irritans*, anterior third.

Fig. 11. Transverse section through the rostrum of *Notonecta glauca*, basal third.

- Fig. 12.* Front view of the head of *Cicada* sp. *pl*, plates with which the maxillæ articulate.
- Fig. 13.* Transverse section through the proboscis of *Sarcopsylla penetrans*, middle.
- Fig. 14.* Transverse section through the rostrum of *Notonecta glauca*, apex.
- Fig. 15.* Transverse section through the proboscis of *Pulex irritans*, base.

VI.—*New Investigations on the Development of the Viviparous Aphides.* By Dr. OTTO ZACHARIAS *.

SINCE the appearance of Metschnikoff's 'Embryologische Studien an Insecten' (1866) the development of the embryo of the viviparous Aphides has not again been made the subject of a monographic investigation. What the Russian author established with regard to the mode of development of the "pseudova" of *Aphis Rosæ* and *A. Pelargonii* passes pretty generally for all that is observable at present. Metschnikoff's description of the development of Aphides (at least in its fundamental features) is regarded as a "rocher de bronze," which presents no point of attack for an incisive criticism. This, however, is not the case, and I will, in a memoir that will appear very shortly, furnish the proof that Metschnikoff's description of the *first* developmental stages (as far as the formation of the S-shaped germinal streak, and even somewhat later) by no means agrees with the facts. For the subsequent stages I have also obtained quite different results of investigation, which I shall venture to summarize at the conclusion of this preliminary note.

The observation of the embryonic development of the viviparous Aphides is for many reasons a difficult matter. Besides the minuteness and delicacy of the objects with which we have to do, there is a third condition which causes many obstacles to the investigation, namely the clearness and strong refractive power of the protoplasmic contents of the egg. If in the case of the eggs of many other insects we have to contend with the obscurity of their yolk, it is in the Aphides the crystal clearness of the latter which frequently acts very prejudicially: prejudicially, inasmuch as under the circumstances indicated the upper half of the egg constantly acts upon the lower half (or *vice versâ*), like a lens with a very short focus, and not only enlarges but also distorts those

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